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Ecological Partitioning by Antbirds of a Moist Tropical Forest in Amazonian Ecuador.

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ECOLOGICAL PARTITIONING BY ANTBIRDS OF A MOIST TROPICAL FOREST IN AMAZONIAN ECUADOR

A Dissertation

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ABSTRACT

From September 1975 through November 1976, the ecological partitioning of a primary moist tropical forest by 26 species of antbirds (Aves: Formicariidae) was studied at Limoncocha, in equatorial Amazonian Ecuador. The antbirds subdivided their habitat by foraging at different forest strata, selecting different foliage densities, and consuming various-sized prey items. At Limoncocha, where daylength, rainfall, temperature, insect population sizes, and herbal flowering cycles showed almost no seasonality, the antbirds bred all year.

INTRODUCTION

From September 1975 through November 1976, I studied a community of 26 antbirds (Aves: Formicariidae), all inhabitants of a primary moist tropical forest, at Limoncocha, in the east-central lowlands of Ecuador. Limoncocha was chosen as the study area because of its tropical location and because it has one of the most aseasonal climates in the world. This avian community seemed ideal for a study of habitat partitioning. In such an unfluctuating environment, questions for investigation included whether breeding time is used as a mechanism for niche partitioning, if more than one species can occupy a niche, and why there are so many more species in the tropics than in the temperate zone. By studying antbird breeding seasons and by analysing antbird morphology related to trophic strategies, I attempted to find answers to these questions.

MATERIALS AND METHODS

The study area (Fig. 1) was near Limoncocha ($0^{o}24'S$, $76^{o}37'W$; 300 m elev.), a small village in east-central Ecuador, bordered by the Rio Jivino on the west and an oxbow lake formed by the Rio Napo on the east. The area was largely composed of relatively undisturbed moist tropical forest (sensu Holdridge 1967) at the time of my study.

To avoid overcollecting, which could possibly affect breeding cycles, I divided the study area into 10 sectors (Fig. 1). Ten to 20 nets were set in each sector during the months noted in Fig. 1. The nets were up roughly eight hours, six days each week. Each month a few antbirds were also shot in forest areas outside all monthly sectors. From March through August 1976, I color banded antbirds, coding them for the sector in which they were caught and released.

Breeding activity by antbirds was defined by the presence of active nests, eggs in the ovary or oviduct, ruptured follicles, oviducts more than 3 mm wide, testis size over 30 mm^2, and by the presence of juveniles which completely lacked skull ossification and contained the

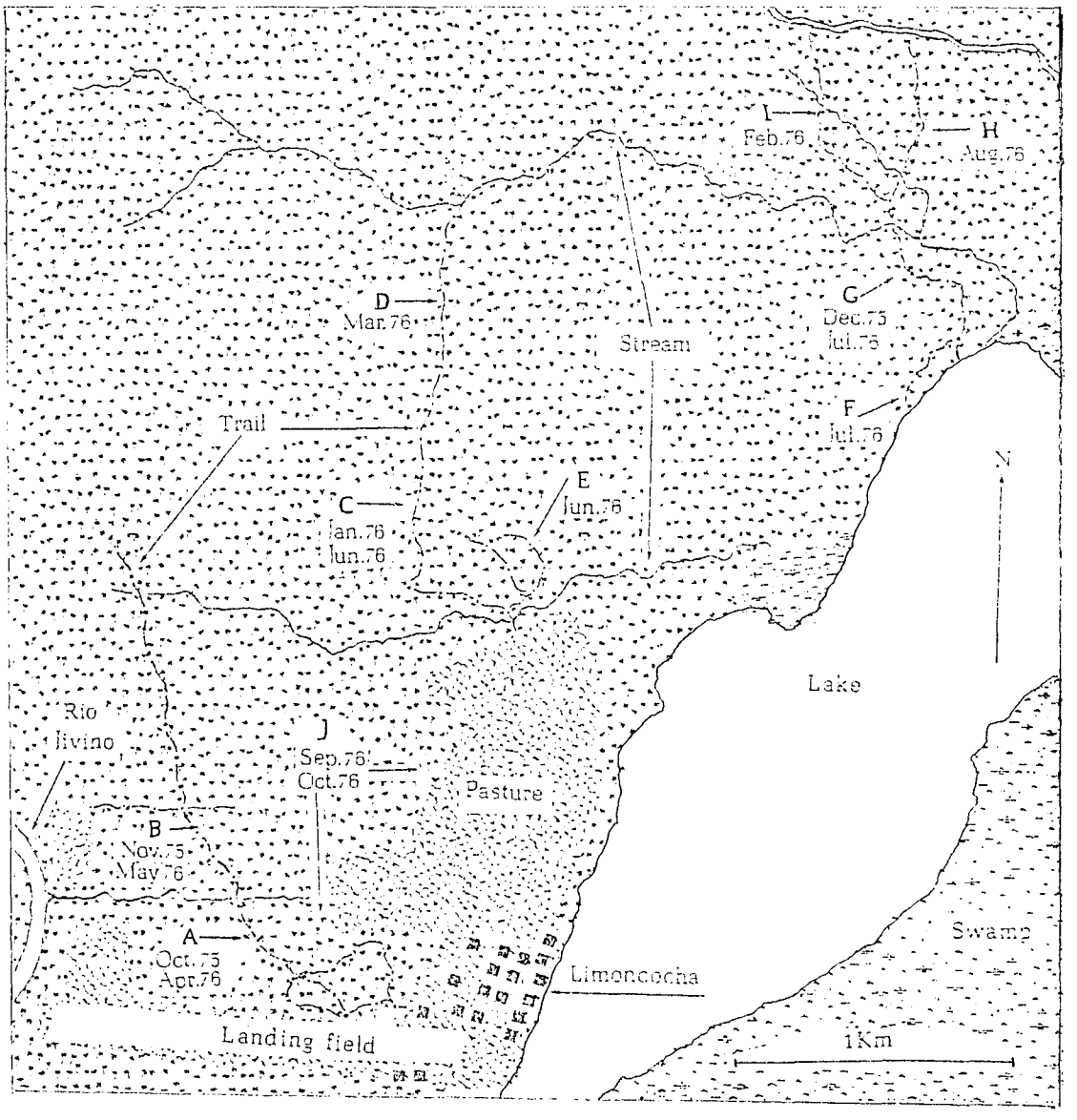
Bursa of Fabricius (for methods with juveniles see Nero 1951, Naik and Andrews 1966, and Benson 1962; for testis size as an indication of breeding time see Moreau 1966 and Foster 1975). Because molt and breeding seldom occur simultaneously, I noted the presence or absence of molt on all specimens.

During monthly aerial surveys 150 m above the forest, notes and photographs were taken to assertain the relative flowering condition of the forest canopy. Erika Tallman recorded the flowering time for 46 species of herbs and low trees in the primary forest from October 1975 through September 1976. From November 1975 through October 1976, insect samples were taken on sunny afternoons at the same region of the study sector B, ca. 1.5 km WNW of Limon-cocha (Fig. 1). The insects were captured with 300 sweeps of a 47.5 cm diameter net mounted on a 121.9 cm pole.

In the morphometric portion of this study, the following measurements were used: bill length=exposed culmen; tarsus length=distance from the back of the tibio-tarsus/tarso-metatarsus joint to the first complete scute above the toes; wing length=distance from the wrist to the tip of an unflattened wing's longest primary. Body weight was taken in grams with a Pesola spring scale.

The taxonomic nomenclature adopted in this study is that of Meyer de Schauensee (1966). In making subspecific determinations, I relied on information contained in Zimmer (1931a, 1931b, 1932a, 1932b, 1932c, 1932d, 1932e, 1932f, 1933a, 1933b, 1933c, 1934, 1937, 1944), Cory and Hellmayr (1924), and on specimens in the Lousiana State University Museum of Zoology.

Figure 1. Map of the vicinity of Limoncocha, Ecuador. On the map are shown the sectors (A-J) into which the study site was divided. Study dates are indicated below each sector label.


I
Feb.76
H
Aug.76
D
Mar.76
Stream
G
Dec.75
Jul.76
F
Jul.76
Trail
E
Jun.76
C
Jan.76
Jun.76
N
Lake
Rio
Jivino
J
Sep.76
Oct.76
Pasture
B
Nov.75
May 76
A
Oct.75
Apr.76
Limoncocha
Swamp
Landing field
1Km

SELECTED PHYSICAL AND BIOLOGICAL FEATURES OF LIMONCOCHA

Climate.-- Except for the fact that June and July tended to be more generally overcast than the other months of the year, my data support Pearson's (1977a) assertion than Limoncocha is climatically aseasonal. Indeed, Limoncocha has one of the most unfluctuating climates in the world. Average monthly temperatures ranged from only 24.1 to 25.6° C (Pearson 1972). A compilation of 14 years of data (1961 to 1975) collected by the Jungle Aviation and Radio Service (Waxhaw NC) showed no pronounced dry or wet seasons. Average total rainfall was 3100 mm with an average monthly total of 258.5 mm. This latter figure is remarkable since 3100 mm/12=258.3 mm. An average minimum rain (191.6 mm) fell in February and an average maximum (313.1) occurred in May. However, any month is potentially the wettest of the year.

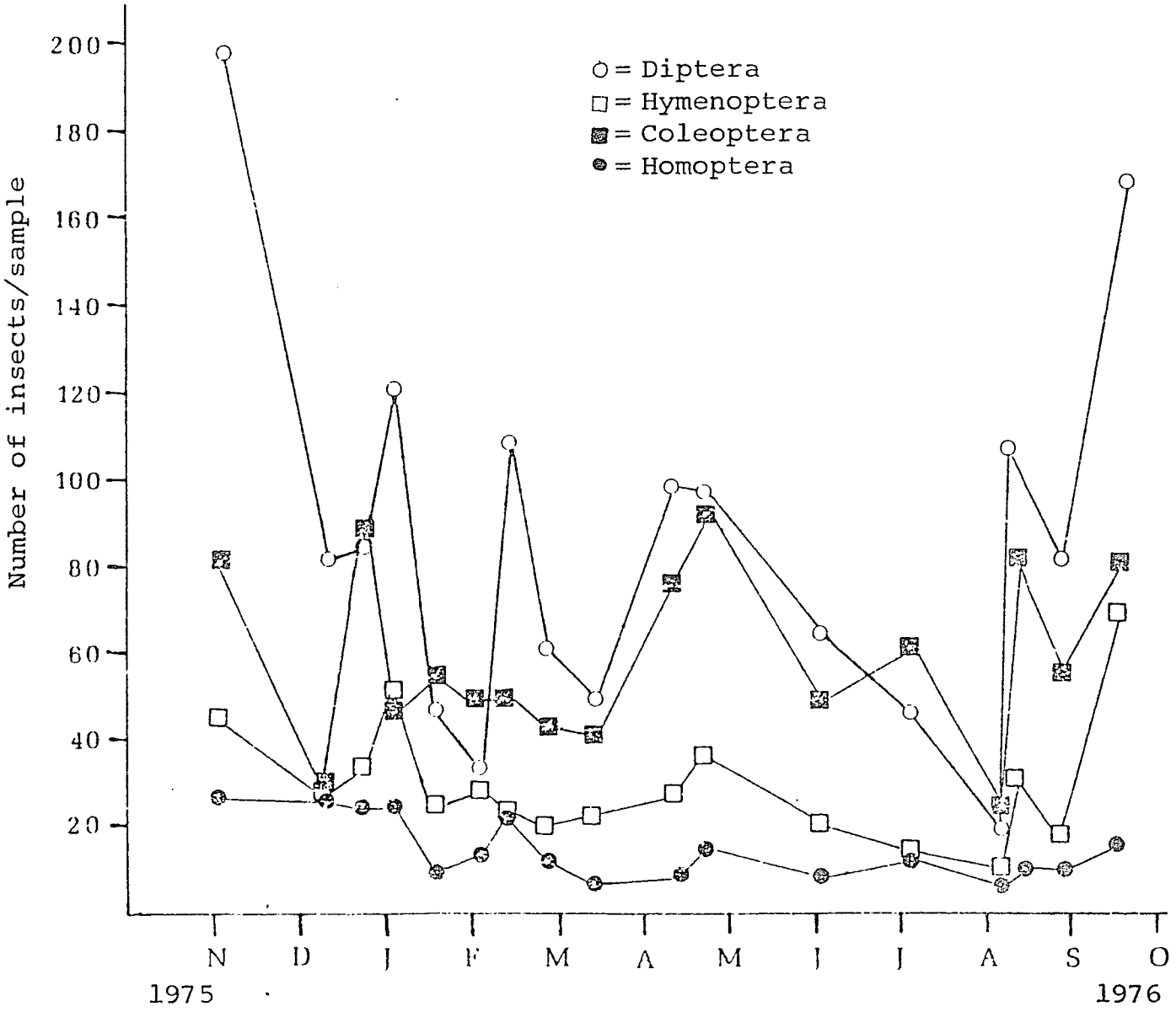
Vegetation.— Pearson (1977b) described the Limoncocha canopy, like that of many tropical forests (Richards 1952, Miller 1963, Moreau 1966), to be a mixture of trees whose fruiting is either year-round or synchronized but occurring acyclically throughout the year. However, I recorded a large number of trees in flower from October

through December and a peak of leafless trees from June through September. At least during my study, leaflessness and flowering corresponded with periods of overcast skies (for leaflessness) and a return of sunshine (for flowering). These correlations agree with Janzen's (1967) observations in Central America.

Over half of the 46 species of herbs and low trees catalogued by Erika Tallman flowered all year. Because of the patchy distribution of tropical plants, other species that flowered all year may have been overlooked. Since they are usually shaded by upper levels, lower strata plants are less affected by cloudiness than are canopy species.

Insects.— Except for dipterans, Limoncocha insects remained at fairly constant numbers throughout the year (Fig. 2) in contrast to other tropical areas which have greatly reduced insect numbers during dry seasons (Davis 1971, Janzen 1973, Wolda 1977, 1978). Pearson (1977b) made similar observations regarding damselflies, dragonflies and tiger beetles at Limoncocha. Dipterans, however, tend to have patchy distributions near carrion and dung. Tabanids may be truly cyclic at Limoncocha: I noticed more of these biting flies in both Octobers of my

Figure 2. Abundance estimates for the four major taxa of insects from the study site (Fig. 1, sector B) ca. 1.5 km WNW Limoncocha, Ecuador.


Number of insects/sample
200
180
160
140
120
100
80
60
40
20
○ = Diptera
□ = Hymenoptera
▩ = Coleoptera
● = Homoptera
N
D
J
F
M
A
M
J
J
A
S
O
1975
1976

study. My data support Jones' (1977) statement that, in the tropical forest understory, insect populations are low.

Birds.— Pearson (1972) reported 347 species of birds at Limoncocha; during this study, my companions and I found 117 additional species, including 13 previously unrecorded from Ecuador (Tallman and Tallman 1977). This diversity is greater than that of other locations of similar elevation, such as Tumi Chucua, Bolivia (313 species)(Pearson 1975b), Yarinacocha, Peru (402 species) (O'Neill and Pearson 1974), Balta, Peru (417 species) (O'Neill, 1974, Ph.D. diss., Louisiana State University), and is perhaps only equalled by that at Tambopata, Peru (O'Neill, pers. comm.). The factors contributing to Limoncocha's avian diversity include its equatorial location, its relatively rich soil, and the probability that it served as a forest refugium during the climatically unstable Quaternary (Haffer 1969, Vanzolini 1973).

Table 1 contains a complete list of Limoncocha antbirds. Here I have commented on each species' status and have included meristic characters related to trophic strategies for those species which inhabit primary forest. These data pertain to females since large series of males were not taken.

Limoncocha does not boast the highest number of antbird species in the world. Balta, Peru, has four species more than Limoncocha. Species missing from Limoncocha but present elsewhere in Ecuadorian lowlands include Pithys albifrons, Rhegmatorhina melanosticta, and Microrhopias quixensis.

Most Limoncocha antbirds appear to have relatively large populations of sedentary individuals. I color banded 150 antbirds of 20 species; 19 (12%) were retrapped but only two retrapped birds (10%) were found outside their original sector of banding. These latter birds were caught in sectors immediately adjacent to the sector where they were banded.

Behaviorally, Limoncocha antbirds are similar to antbirds in other locations (see Willis 1966 , 1967, 1968, 1969, Pearson 1977a, and Jones 1977). A wide range of dependence on army ant swarms exist, with some species being nondependent while others are obligate ant followers. Although some Limoncocha antbirds had similar feeding habits, they maintained distinct trophic positions.

Table 1. Meristic characters and comments on the status and habitats of Limoncocha antbirds. N: range (mean $\pm$ 1 SD). Weights are in grams, linear measurements are in millimeters.

1) Cymbilaimus lineatus intermedius

uncommon in primary forest.

weight: 2:36.0-38.0(37.0 ± 1.4)

bill: 4:21.7-22.2(21.93 ± 0.26)

wing/weight: 4:1.9-2.1(2.025 ± 0.096)

tarsus/weight: 4:0.6-0.7(0.675 ± 0.050)

2) Frederickena unduligera fulva

uncommon in primary forest.

weight: 1:81(81 ± 0)

bill: 3:26.5-27.5(26.93 ± 0.51)

wing/weight: 3:1.2-1.2(1.2 ± 0.0)

tarsus/weight: 3:0.4-0.4(0.4 ± 0.0)

3) Taraba major melanurus

common but restricted to secondary growth.

4) Thamnophilus schistaceus capitalis

common in primary forest.

weight: 7:19.5-25.0(21.4 ± 1.8)

bill: 10:17.3-18.6(18.01 ± 0.396)

wing/weight: 10:2.7-3.2(2.91 ± 0.396)

tarsus/weight: 10:0.9-1.0(0.91 ± 0.032)

5) Thamnophilus murinus ssp.

not observed during this study, although previously reported at Limoncocha and common elsewhere in eastern Ecuador.

6) Pygiptila stellaris maculipennis

common in primary forest

weight: 7:22-26(23.9 ± 1.4)

bill: 4:19.8-20.8(20.425 ± 0.435)

wing/weight: 4:3.1-3.2(3.125 ± 0.05)

tarsus/weight: 4:0.7-0.8(0.733 ± 0.058)

7) Neoctantes niger

uncommon in primary forest.

weight: 2:29.0-30.0(29.5 ± 0.7)

bill: 3:16.5-17.9(17.33 ± 0.737)

wing/weight: 3:2.3-2.3(2.3 ± 0.0)

tarsus/weight: 3:0.7-0.8(0.733 ± 0.577)

8) Thamnomanes ardesiacus ardesiacus

common in primary forest.

weight: 12:15.0-20.5(19.9 ± 1.4)

bill: 16: 15.0-17.8(16.375 ± 0.724)

wing/weight: 16:3.5-4.0(3.83 ± 0.126)

tarsus/weight: 16:1.0-1.1(1.006 ± 0.025)

9) Thamnomanes caesius glaucus

common in primary forest.

weight: 16:13.0-19.0(16.3 ± 1.7)

bill: 14:15.3-17.4(16.729 ± 0.578)

wing/weight: 14:3.9-4.3(4.079 ± 0.131)

tarsus/weight: 14:0.9-1.2(1.29 ± 0.073)

10) Myrmotherula brachyura brachyura

although observed in primary forest, only one immature of this rare or uncommon species was collected from secondary growth.

11) Myrmotherula surinamensis multostriata

common but restricted to the lakeshore and banks of larger rivers; not observed within primary forest.

12) Myrmotherula hauxwelli suffusa

common in primary forest.

weight: 22:7.0-13.0(10.4 ± 1.4)

bill: 19:12.3-14.4(13.379 ± 0.56)

wing/weight: 19:4.5-4.9(4.732 ± 0.129)

tarsus/weight: 19:1.4-1.9(1.711 ± 0.115)

13) Myrmotherula ornata saturata

common in primary forest.

weight: 9:8.0-10.2(9.3 ± 0.7)

bill: 10:13.6-14.7(14.22 ± 0.418)

wing/weight: 10:5.1-5.5(5.26 ± 0.117)

tarsus/weight: 10:1.6-1.8(1.68 ± 0.063)

14) Myrmotherula erythrura erythrura

rare in primary forest; collected once during this study: 18 Oct. 1976.

15) Myrmotherula axillaris melaena

common in primary forest.

weight: 9:6.0-13.0(8.3 ± 2.1)

bill: 12: 12.2-14.2(13.308 ± 0.629)

wing/weight: 12:5.7-6.3(5.975 ± 0.166)

tarsus/weight: 12:1.6-1.9(1.775 ± 0.087)

16) Myrmotherula schisticolor interior

rare in primary forest; perhaps a stray from the upper subtropical zone (Meyer de Schauensee 1966) and previously unrecorded from Limoncocha. Collected 11 Feb., 4 and 5 Aug. 1976.

17) Myrmotherula longipennis zimmeri

rare in primary forest; only observed once when an immature was collected on 12 April 1976.

18) Myrmotherula sunensis sunensis

rare in primary forest; two females taken (11 and 13 Aug. 1976) both in breeding condition.

19) Myrmotherula menetriesii pallida

common in primary forest.

weight: 2:7.0-7.5(7.3 ± 0.4)

bill: 4:13.5-14.8(13.975 ± 0.568)

wing/weight: 4:6.9-7.0(6.925 ± 0.05)

tarsus/weight: 4:1.9-2.1(2.05 ± 0.1)

20) Cercomacra cinerascens cinerascens

rare in primary forest; only one collected: 9 Jan. 1976. Pearson (1972) considered this species to be common.

21) Cercomacra nigrescens aequatorialis

rare in primary forest; one specimen, 22 July 1976, is the only Limoncocha record and was obtained at a stream edge.

22) Cercomacra serva serva

rare in primary forest. Two specimens, 1 Jan. and 25 Mar. 1976, represent the only Limoncocha records.

23) Myrmoborus myotherinus napensis

common in primary forest.

weight: 11:18.0-22.0(19.9 ± 1.5)

bill: 14:15.7-16.9(16.22 ± 0.36)

wing/weight: 14:2.8-3.1(2.986 ± 0.086)

tarsus/weight: 14:1.2-1.3(1.271 ± 0.047)

24) Hypocnemis cantator saturata

common in primary forest.

weight: 3:10.0-13.8(11.8 ± 1.9)

bill: 4:14.8-15.2(15.025 ± 0.206)

wing/weight: 4:4.3-4.4(4.375 ± 0.05)

tarsus/weight: 4:1.5-1.7(1.6 ± 0.082)

25) Percnostola leucostigma subplumbea

common in primary forest.

weight: 8:23.5-28.0(27.1 ± 2.5)

bill: 11:17.7-19.8(18.94 ± 0.61)

wing/weight: 11:2.3-2.5(2.372 ± 0.065)

tarsus/weight: 11:0.9-1.0(0.918 ± 0.040)

26) Sclateria naevia argentata

common in primary situations but restricted to the immediate vicinity of water.

27) Myrmeciza hyperythra

common in primary forest.

weight: 9:37.0-47.0(39.9 ± 3.8)

bill: 6:23.4-25.4(24.283 ± 0.828)

wing/weight: 6:1.9-2.0(1.983 ± 0.041)

tarsus/weight: 6:0.7-0.8(0.717 ± 0.041)

28) Myrmeciza melanoceps

common but restricted to secondary growth.

29) Myrmeciza fortis fortis

uncommon in primary forest.

weight: 8:48.0-57.0(51.6 ± 3.4)

bill: 7:22.2-23.3(22.67 ± 0.36)

wing/weight: 7:1.5-1.6(1.51 ± 0.038)

tarsus/weight: 7:0.6-0.7(0.671 ± 0.049)

30) Myrmeciza atrothorax ssp.

One specimen collected 20 July 1976 is the only Limoncocha record.

31) Gymnopithys leucaspis castanea

common in the primary forest.

weight: 10:20.0-28.2(24.4 ± 2.8)

bill: 7:17.1-18.0(17.56 ± 0.395)

wing/weight: 7:2.6-2.9(2.771 ± 0.095)

tarsus/weight: 7:1.0-1.1(1.014 ± 0.038)

32) Hylophylax naevia theresae

common in primary forest.

weight: 17:11.0-16.0(13.1 ± 1.1)

bill: 14:15.3-17.1(16.114 ± 0.643)

wing/weight: 14:4.2-4.6(4.457 ± 0.102)

tarsus/weight: 14:1.3-1.6(1.479 ± 0.089)

33) Hylophylax poecilonota lepidonota

common in primary forest.

weight: 4:15.5-18.0(16.6 ± 1.1)

bill: 8:17.0-17.8(17.338 ± 0.297)

wing/weight: 8:3.5-3.8(3.675 ± 0.104)

tarsus/weight: 8:1.1-1.4(1.263 ± 0.092)

34) Phlegopsis nigromaculata nigromaculata

common in primary forest.

weight: 10:40.0-51.0(47.8 ± 3.7)

bill: 7:20.7-22.7(21.34 ± 0.69)

wing/weight: 7:1.7-1.8(1.786 ± 0.038)

tarsus/weight: 7:0.6-0.7(0.614 ± 0.038)

35) Phlegopsis erythroptera erythroptera

uncommon in primary forest.

weight: 6:46.0-70.0(59.5 ± 8.1)

bill: 6:19.1-22.0(20.27 ± 1.34)

wing/weight: 6:1.4-1.5(1.417 ± 0.041)

tarsus/weight: 6:0.5-0.6(0.533 ± 0.52)

36) Chamaeza nobilis rubida

common in primary forest.

weight: 4:130.0-148.0(138.9 ± 8.4)

bill: 4:22.7-23.1(22.975 ± 0.19)

wing/weight: 4:0.7-0.8(0.75 ± 0.058)

tarsus/weight: 4:0.3-0.3(0.3 ± 0.0)

37) Formicarius colma nigrifrons

common in primary forest.

weight: 4:41.0-45.0(42.8 ± 1.7)

bill: 12:17.6-20.0(18.783 ± 0.845)

wing/weight: 12:1.8-2.0(1.917 ± 0.072)

tarsus/weight: 12:0.6-0.7(0.692 ± 0.029)

38) Formicarius analis zamorae

common in primary forest.

weight: 10:44.0-51.0(49.9 ± 3.9)

bill: 13:18.4-20.5(19.292 ± 0.669)

wing/weight: 13:1.6-1.8(1.69 ± 0.056)

tarsus/weight: 13:0.6-0.6(0.6 ± 0.0)

39) Myrmothera campanisona signata

common in primary forest.

weight: 2:39.0-46.0(42.5 ± 4.9)

bill: 4:18.5-19.6(19.1 ± 0.535)

wing/weight: 4:1.8-1.9(1.825 ± 0.05)

tarsus/weight: 4:0.9-1.0(0.95 ± 0.058)

40) Conopophaga aurita occidentalis

common in primary forest.

weight: 4:22.0-29.0(24.9 ± 3.0)

bill: 7:13.1-14.7(13.9 ± 0.548)

wing/weight: 7:2.4-2.7(2.557 ± 0.113)

tarsus/weight: 7:1.0-1.1(1.042 ± 0.053)

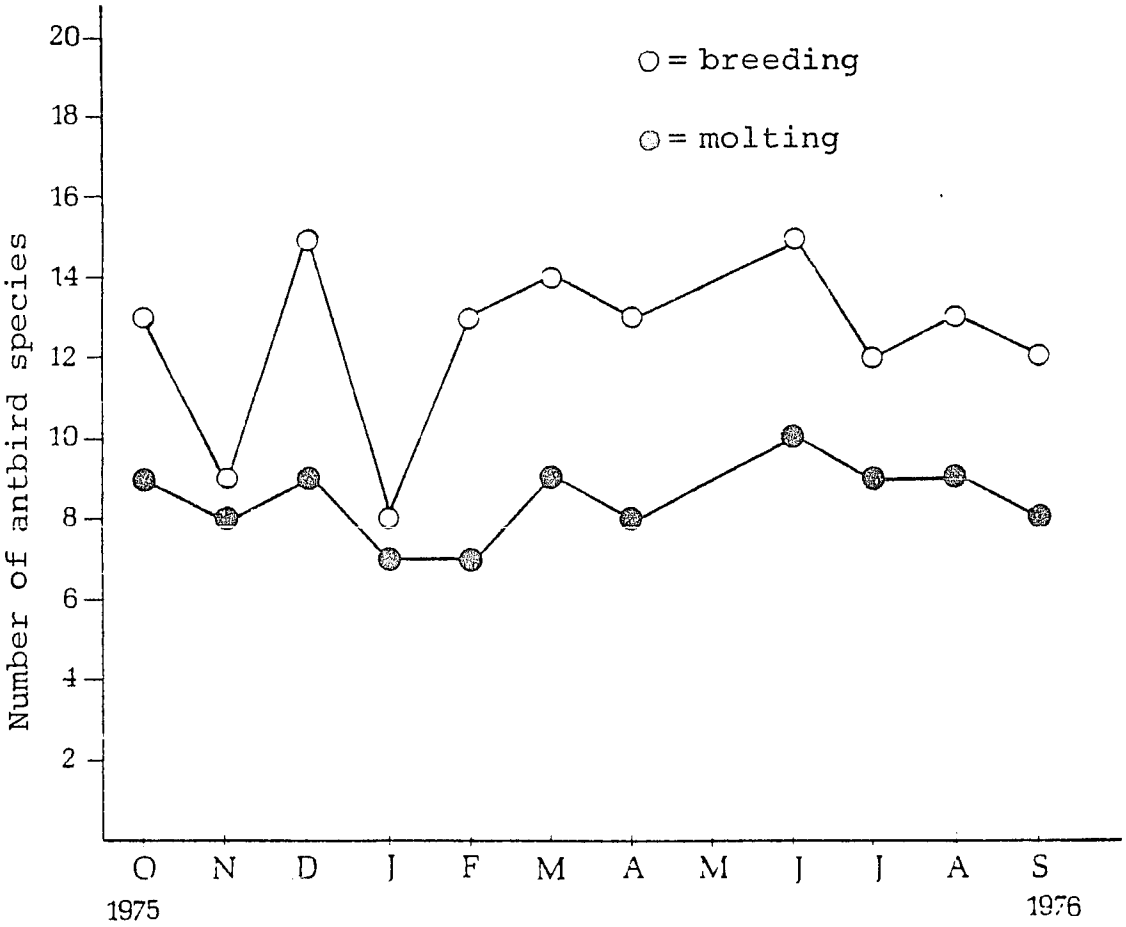
ANTBIRD BREEDING

The forest-inhabiting antbirds at Limoncocha appeared to breed all year without showing peaks of reproductive activity (Fig. 3; Table 2). Among the female antbirds collected, the monthly average of breeders was 55% with a range from 42% in July to 76% in April.

Coupled with the breeding data, the aseasonality of molt and the high incidence (33%) of individual birds molting and breeding simultaneously indicate noncyclic breeding by Limoncocha antbirds. In most other birds, the onset of prebasic molt is the most dependable evidence of the cessation of breeding cycles, even in species showing a low year-round incidence of breeding (Tordoff and Dawson 1965). The physiological demands of molt usually preclude molting and breeding at the same time. Low molt frequency has been used to determine peaks of breeding activity in other South American bird populations (Miller 1963, Snow and Snow 1964, Davis 1971, Snow 1976). Presumably Limoncocha antbirds are able to breed and molt simultaneously because molting occurs so slowly that it is not a significant energy drain on breeders.

My finding of acyclic breeding by Limoncocha antbirds

Figure 3. Composite molt and breeding activity of Limon-
cocha antbirds.


○ = breeding
○ = molting
Number of antbird species
20
18
16
14
12
10
8
6
4
2
O
N
D
J
F
M
A
M
J
J
A
S
1975
1976

in the primary forest is an unexpected discovery. Almost all forest birds, including antbirds, are seasonal breeders; around the world, species known to breed all year are second growth inhabitants or waterbirds (Burger 1949, Thompson 1950, Skutch 1950, Betts 1952, Davis 1953, Miller 1955, 1958, Marchant 1960, Benson 1962, Snow and Snow 1964, Ricklefs 1966, Willis 1967, 1968, 1969, Haverschmidt 1968, Harris 1974, Snow 1966, 1976). For example, the antbird, Gymnopithys leucaspis, is seasonal in Panama, where dry seasons exist (Willis 1967), but breeds throughout the year at Limoncocha.

The worldwide prevalence of avian breeding cycles has been attributed to several major factors: 1) climatic fluctuations which cause seasons and cycles of base resources; 2) birds' high metabolic rates that favor reduction of activities not directly involved with feeding; 3) presence of resident or migrant competitors; 4) tactics for reducing predation (at a given time, a fewer percent of the breeding population is taken by predators in seasonal species); and 5) mechanisms for assuring group and pair readiness for breeding (Elliot 1950, Miller 1963, Immelmann 1971). Limoncocha's remarkable resource stability is a major factor contributing to the aseason-

ality of its antbird breeding. But why any of the other factors do not cause breeding seasons is obscure. Prey populations must not only be stable but also quite diverse since, as pointed out earlier, the population of any one species is not particularly high. The impact of migrant birds in lowland South America, including Limoncocha, is much less than at higher elevations (Leck 1972); Willis (1966) found that Panamanian antbirds breed when migrants are most abundant. Limoncocha antbirds apparently occur in sufficient numbers that meetings between reproductively compatible individuals are assured without predation seriously affecting the breeding population.

Table 2. Breeding data for antbirds suspected of year-round nesting. (The following subscripts are employed: ♀=breeding female or active nests; ♂ = testis greater than 30 mm^2; ?=bird possibly breeding; i=fledgling or immature; *=molt present; *=molting and breeding simultaneously).

species	type of evidence	1975 Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	1976 Aug.	Sep.
Cymbilaimus lineatus	breeding	?♀				X♀				X♀			
	molting	*	*		*					*			
Thamnophilus schistaceus	breeding	X♀	X♀	X♀		X♀				X♀	X♀		
	molting	*		*						*			
Thamnomanes ardesiacus	breeding	X♀		?♀	X_i	X♀		X♀	X♀	X♀	X♀	X♀	X♀
	molting	*	*			*	*	*	*	*		*	
Thamnomanes caesius	breeding	X♀i		X_i			X_i	X_i	X♀		X♀	X♀	
	molting			*			*				*	*	
Myrmotherula hauxwelli	breeding	X_i	X_i		X♀	X_i		X♀	X♀			X♀	?♀
	molting	*	*		*	*	*				*	*	*
Myrmotherula ornata	breeding			X♀		X♀	X_i		X_i	?♀	X♀		
	molting	*		*	*	*				*	*	*	
Myrmotherula axilaris	breeding	X♀			X_i	X♀	X♀	X_i		X♀		X♀	X♀
	molting	*	*	*	*			*				*	

species	type of evidence	1975 Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	1976 Aug.	Sep.
Myrmotherula menetriesii	breeding						X_i			X_i			X_i
	molting	*				*	*	*				*	*
Myrmoborus myotherinus	breeding		?♀	X_i	?♀	$X_♀$			$X_♀$	X_i	X_i	$X_♀$	$X_♀$
	molting						*	*	*				*
Hypocnemis cantator	breeding	X_i		$X_♀$				$X_♀$				$X_♀$	$X_♀$
	molting				*								*
Percnostola leucostigma	breeding	X_i					X_i	X_i	X_i	$X_♀$	$X_♀$		
	molting	*	*		*		*			*	*	*	
Myrmeciza hyperythra	breeding	$X_♀$		$X_♀$				$X_♀$			X_i		$X_♀$
	molting			*				*			*		*
Myrmeciza melanoceps	breeding	$X_♀$	X_i			$X_♀$					X_i	X_i	$X_♀$
	molting			*							*		
Myrmeciza fortis	breeding	$X_♀$	X_i	X_i	X_i		X_i	$X_♀$		$X_♂$			
	molting		*							*			

Species	type of evidence	1975 Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	1976 Sep.
Gymnopithys leucaspis	breeding	$X_{♀}$		X_{i}	X_{i}		$X_{♀}$	$X_{♀}$	X_{i}	X_{i}		X_{i}	
	molting			*		*			*	*	*		*
Hylophylax naevia	breeding	$X_{♀}$		X_{i}	X_{i}		X_{i}	$X_{♀}$	X_{i}	X_{i}	$X_{♀}$	$X_{♀}$	$X_{♀}$
	molting	*				*			*				*
Hylophylax poecilonota	breeding			$X_{♀}$		$X_{♀}$				X_{i}	$X_{♀}$		
	molting		*			*	*		*				
Phlegopsis nigromaculata	breeding	$X_{♀}$	$X_{♀♂}$		$X_{♂}$	$X_{♂}$	$X_{♀♂i}$			X_{i}	?	$X_{♂}$	$X_{♂}$
	molting	*	*	*	*			*		*	*	*	*
Phlegopsis erythroptera	breeding	$X_{♀}$	$X_{♀}$	$X_{♀}$			$X_{♀}$		$X_{♀}$	$X_{♀}$			
	molting	*					*			*			
Chamaeza nobilis	breeding	X_{i}	$X_{♂i}$	X_{i}	$X_{♀}$		X_{i}	$X_{♂i}$					X
	Molting							*					
Formicarius colma	breeding	$X_{♂i}$	$X_{♂}$	$X_{♂i}$	$X_{♀♂}$	$X_{♀♂}$	$X_{♀}$	$X_{♂}$			$X_{♂i}$	X_{i}	
	molting	*			*			*			*		

species	type of evidence	1975 Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	1976 Aug.	Sep.
Formicarius analis	breeding	$X_{♂}$	X_i	$X_{♂i}$		$X_{♂♀}$	$X_{♀}$	$X_{♀}$		X_i	X_i	X_i	$X_{♀♂}$
	molting	*		*					*			*	
Conopophaga aurita	breeding	$X_{♀}$		X_i		X_i	$X_{♀}$		X_i			$X_{♀}$	
	molting			*						*			

HABITAT PARTITIONING BY LIMONCOCHA ANTBIRDS

The environmental stability of aseasonal locations insures that the habitats are filled to carrying capacity and that there is strong selection for niche partitioning (MacArthur 1971). Because birds respond to environmental cues for synchronizing breeding, I had suspected that Limoncocha antbirds, lacking such cues, might develop breeding seasons in response to interspecific competition (for a discussion of the use of breeding time for niche partitioning, see Cody 1974, Lack 1950, Klopfer 1973, Ricklefs 1966, Immelmann 1971, and MacArthur 1964, 1971). Finding that most antbirds at Limoncocha bred throughout the year, I turned to an analysis of morphological characters to define the birds' niche positions.

Morphology can be used as an index to a bird's trophic position in its habitat (Ricklefs and Cox 1977). Bill length reflects the relative size of prey items consumed (Keast 1968, Cody 1974). The tarsus length/body weight ratio indicates differences in substrate utilization (Grant 1965, Fretwell 1969). Species with relatively longer tarsi inhabit less dense habitats than do ones with shorter tarsi (Pearson 1977a). The wing length/body

weight ratio mirrors the relative breadth of foraging height in the forest strata (Pearson 1977a) and possibly also substrate density (Hamilton 1961). Longer-winged birds have a broader foraging range than shorter-winged species. When two species show similar wing/weight ratios, one must carefully investigate their positions in the forest since it cannot be assumed that their actual foraging strata are at the same heights.

All Limoncocha antbird species occupy discrete trophic niches. If at least one variable shows nonoverlap, the species involved are assumed not to occupy the same trophic niche. Of 325 possible species comparisons between nonrare, female, primary forest-inhabiting antbirds, 63% showed no overlap of bill sizes, wing/weight and tarsus/weight ratios. An additional 35% of the species pairs exhibited nonoverlap in at least one variable (Table 3). Only four pairs showed overlap in all three parameters: Thamnomanes schistaceus/Gymnopithys leucaspis, Formicarius colma/F. analis, Thamnomanes ardesiacus/Hylophylax poecilonota, and Thamnomanes ardesiacus/T. caesius. The first three pairs only show slight overlap (less than 9%) in tarsus/weight ratios. Furthermore, T. schistaceus and G. leucaspis, apparently having similar foraging breadths,

were seen in the field to forage at different heights: T. schistaceus was found higher than the ground-hugging G. leucaspis. A similar situation exists for T. ardesiacus and H. poecilonota: the former was usually observed at more than 3 m height in the forest while the latter was seldomly seen over 1 m above the ground. The similarity in the wing/weight ratios of F. colma and F. analis is less than expected for two ground-walking species and may be affected by different foliage densities in the birds' habitats. Although both species are forest-floor foragers, the overlap between their tarsus/weight ratios is very slight (1%). The relatively longer-tarsied F. colma occurred in the less tangled primary forest while F. analis inhabited the denser, more disturbed areas. Thamnomanes ardesiacus and T. caesius are remarkably similar. I detected no difference between the species' foraging strategies. They were equally common from 1 to 7 m and often were caught together in the same nets. Pearson (1975) thought them both common salliers in the lower strata. However, the wing/weight ratios of the two species approach, but do not exceed, the theoretical limit to niche overlap. This limit occurs, along critical gradients, at the point where the difference between each

species' means equals the standard deviation (SD) of either competitor (MacArthur 1972, May and MacArthur 1972). The difference between the means of the wing/weight ratios of the two species and the SD of T. caesius is + 0.11 mm. Despite these similarities, these species have historically been placed in different genera. Although T. ardesiacus has been classified as belonging to the genera Thamnophilus, Hypocnemis and, most recently, Dysithamnus, my study is in agreement with Meyer de Schauensee (1966) who is one of the few authors to remove T. ardesiacus from Dysithamnus. He based his decision on reported similarity in bill structure and behavior.

Table 3. Percent overlap in three morphometric features of antbird species pairs (bill = exposed culmen length, w/wt = wing length/body weight, t/wt = tarsus length/body weight). Species combinations lacking overlap in the three features are omitted.

	bill	w/wt	t/wt
Cymbilaimus lineatus and:			
Pygiptila stellaris	00	00	32
Neoctantes niger	00	00	72
Myrmeciza hyperythra	00	42	36
M. fortis	12	00	00
Phlegopsis nigromaculata	28	00	25
P. erythroptera	14	00	08
Formicarius colma	00	33	56
F. analis	00	00	07
Myrmothera campanisona	00	09	00
Thamnophilus schistaceus and:			
Pygiptila stellaris	00	35	00
Neoctantes niger	29	00	00
Thamnomanes ardesiacus	08	00	05
Thamnophilus schistaceus and:			
Thamnomanes caesius	09	00	14
Myrmoborus myotherinus	00	08	00
Percnostola leucostigma	18	00	69
Gymnopithys leucaspis	30	49	08
Hylophylax poecilonota	16	00	00
Formicarius colma	28	00	00
F. analis	12	00	00
Myrmothera campanisona	12	00	37
Conopophaga aurita	00	27	05
Pygiptila stellaris and:			
Neoctantes niger	00	00	100
Myrmoborus myotherinus	00	15	00
Percnostola leucostigma	08	00	00

	bill	w/wt	t/wt
Pygiptila stellaris and:			
Myrmeciza hyperythra	00	00	61
M. fortis	00	00	30
Phlegopsis nigromaculata	21	00	11
P. erythroptera	72	00	00
Formicarius colma	10	00	35
F. analis	15	00	00
Neoctantes niger and:			
Thamnomanes ardesiacus	26	00	00
T. caesius	36	00	00
Myrmoborus myotherinus	16	00	00
Percnostola leucostigma	14	14	00
Myrmeciza hyperythra	00	00	87
M. fortis	00	00	70

	bill	w/wt	t/wt
Neoctantes niger and:			
Gymnopithys leucaspis	57	00	00
Hylophylax naevia	19	00	00
H. poecilonota	96	00	00
Phlegopsis nigromaculata	00	00	58
Formicarius colma	18	00	82
Thamnomanes ardesiacus and:			
Thamnomanes caesius	49	17	56
Myrmoborus myotherinus	66	00	00
Hypocnemis cantator	08	00	00
Percnostola leucostigma	03	00	09
Gymnopithys leucaspis	16	00	66
Hylophylax naevia	36	00	00
H. poecilonota	17	25	02

	bill	w/wt	t/wt
Thamnomanes ardesiacus and:			
Formicarius colma	06	00	00
Myrmothera campanisona	00	00	25
Conopophaga aurita	00	00	36
Thamnomanes caesius and:			
Myrmoborus myotherinus	32	00	03
Hypocnemis cantator	00	05	00
Percnostola leucostigma	00	00	18
Gymnopithys leucaspis	20	00	65
Hylophylax naevia	34	06	00
H. poecilonota	25	00	39
Myrmothera campanisona	00	00	29
Conopophaga aurita	00	00	70
Myrmotherula hauxwelli and:			
Myrmotherula ornata	19	00	62
M. axillaris	78	00	46
M. menetriesii	32	00	06
Hypocnemis cantator	00	00	31
Hylophylax naevia	00	12	13
H. poecilonota	00	00	02
Conopophaga aurita	36	00	00
Myrmotherula ornata and:			
Myrmotherula axillaris	19	00	28
M. menetriesii	52	00	00
Hypocnemis cantator	00	00	31
Hylophylax naevia	00	00	10
Conopophaga aurita	45	00	00

	bill	w/wt	t/wt
Myrmotherula axillaris and:			
Myrmotherula menetriesii	30	00	07
Hypocnemis cantator	00	00	15
Hylophylax naevia	00	00	05
Conopophaga aurita	34	00	00
Myrmotherula menetriesii and:			
Hypocnemis cantator	09	00	00
Conopophaga aurita	77	00	00
Myrmoborus myotherinus and:			
Gymnopithys leucaspis	00	12	00
Hylophylax naevia	70	00	06
H. poecilonota	00	00	74
Hypocnemis cantator and:			
Hylophylax naevia	00	32	24
Percnostola leucostigma and:			
Gymnopithys leucaspis	09	00	11
Hylophylax poecilonota	04	00	00
Phlegopsis erythroptera	25	00	00
Formicarius colma	70	00	00
F. analis	50	00	00
Myrmothera campanisona	64	00	45
Conopophaga aurita	00	15	09
Myrmeciza hyperythra and:			
Myrmeciza fortis	00	00	34
Phlegopsis nigromaculata	00	00	10

	bill	w/wt	t/wt
Myrmeciza hyperythra and:			
Formicarius colma	00	29	42
Myrmothera campanisona	00	04	00
Myrmeciza fortis and:			
Phlegopsis nigromaculata	10	00	26
P. erythroptera	00	12	09
Chamaeza nobilis	31	00	00
Formicarius colma	00	00	50
F. analis	00	03	08
Gymnopithys leucaspis and:			
Hylophylax naevia	08	00	00
H. poecilonota	46	00	03
Formicarius colma	16	00	00
Gymnopithys leucaspis and:			
Myrmothera campanisona	00	00	28
Conopophaga aurita	00	15	47
Hylophylax naevia and:			
Hylophylax poecilonota	10	00	12
Hylophylax poecilonota and:			
Formicarius colma	10	00	00
Conopophaga aurita	00	00	07
Phlegopsis nigromaculata and:			
Phlegopsis erythroptera	32	00	18
Chamaeza nobilis	03	00	00
Formicarius colma	00	12	12
F. analis	00	16	42

	bill	w/wt	t/wt
Phlegopsis nigromaculata and:			
Myrmothera campanisona	00	34	00
Phlegopsis erythroptera and:			
Formicarius colma	25	00	03
F. analis	47	00	00
Myrmothera campanisona	27	00	00
Formicarius colma and:			
Formicarius analis	45	04	01
Myrmothera campanisona	54	21	00
Formicarius analis and:			
Myrmothera campanisona	62	10	00
Myrmothera campanisona and:			
Conopophaga aurita	00	00	20

ANTBIRD NICHES AND SPECIES DIVERSITY

Limited resources create selection for niche development and segregation between competing species. Limoncocha antbirds, as a group, exploit a wide variety of prey types (Haverschmidt 1968), each with low population numbers. The correlation between high tropical species diversity and low species density is a fundamental difference between the tropical and temperate zones. The diversity of prey items has been used as one explanation as to why there are so many tropical birds (Orians 1969, Hespenheide 1971, Remsen 1978, Ph.D. diss., U. Calif., Berekely). Although a habitat tightly packed with species having small but discrete niches results in these occupants being vulnerable to environmental fluctuations, tropical species diversity is maintained because of the relative climatic stability of the region (MacArthur 1971).

Flemming (1973) claims that fine vertical stratification contributes little to the increase diversity of tropical mammal communities. He attributes high diversity to the presence of many rare species. While his conclusions may also apply to birds (20% of Limoncocha antbirds may be rare), for any two competitors, the variable that

prevents competition is of paramount importance, regardless of how insignificant it may be in the interactions between other species.

Greater species diversity in the tropics may ultimately be attributed to the rise to dominance by angiosperms during the Cretaceous; Raven (1977) suggested that the ability of flowering plants to pollinate over long distances and their coevolution with specific insect vectors resulted in patchy distributions unlike those of preceding floras. If this model for initial community evolution is correct, concomitant evolution of vertebrate predators likely followed the insects' coevolution with the angiosperms.

SUMMARY

This study, conducted from September 1975 through November 1976, is an inquiry into ecological partitioning by a community of 26 antbirds of a primary moist tropical forest. The study site, at Limoncocha in Amazonian Ecuador, is one of the most unfluctuating environments in the world.

Upon making the unexpected discovery that most forest-inhabiting antbirds at Limoncocha bred throughout the year, I used an analysis of morphological characters (bill size, wing length/body weight and tarsus length/body weight ratios) to define the species' trophic niches. Even the most broadly overlapping species pair occupied niches within the theoretical limits hypothesized for avian competitors, which occur along a critical gradient when the means of the two population curves equal either standard deviation.

This study upholds Gause's Rule that no two species occupy the same niche. Also it has taxonomic consequences for two species because, despite being the most similar species at Limoncocha, Thamnomanes caesius and T. ardesiacus have historically been placed in different genera.

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VITA

Born 1 June 1947, Dan Allen Tallman was graduated from the Hawthorne High School (Washington, D.C.) in 1966. He married Erika Jansic and obtained his B.A. from Antioch College in 1971. He and Erika have one son, David, born in 1977.

Under the work/study program at Antioch College, Tallman served as an apprentice to Dr. Allan R. Phillips at the National University of Mexico, as a museum aide at the U.S. National Museum, and as an undergraduate researcher with two grants from the National Science Foundation and one from the Sloan Foundation.

At Louisiana State University, Tallman obtained the M.S. degree in Zoology in August 1974 and he is now a condidate for the Ph.D. in Zoology at the May 1979 commencement. During his years at LSU, Tallman studied the ecology and systematics of birds in Peru and Ecuador.

EXAMINATION AND THESIS REPORT

Candidate: Dan Allen Tallman

Major Field: Zoology

Title of Thesis: Ecological Partitioning by Antbirds of a Moist Tropical Forest in Amazonian Ecuador

Approved:

J. Michael Fitzpatrick
Major Professor and Chairman

James D. Ingraham
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Date of Examination:

7 March 1979